THE PIVOTAL ROLE OF RANK IN GROOMING AND SUPPORT BEHAVIOR IN A CAPTIVE GROUP OF BONOBOS (PAN PANISCUS)

by

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Summary

We investigated dyadic grooming relationships in a captive group of bonobos (*Pan paniscus*) and questioned what social function grooming fulfils in the 'market of services and favors'. Hereto we examined which of two theoretical models — grooming for support (Seyfarth, 1977, 1980) or grooming according to the similarity principle (de Waal & Luttrell, 1986) — best accounted for the observed grooming distribution. Similarity in traits did not correlate with increased grooming or close proximity among the individuals. Therefore, the similarity hypothesis was rejected. Seyfarth's model of rank-related grooming was largely confirmed. The animals distributed their grooming according to the rank of the receivers. We found an exchange between grooming and receipt of support. There was more grooming up than down the hierarchy. However, not all predictions about rank-related competition over grooming were confirmed. We found that dyadic grooming reciprocity indeed increased with decreasing rank distance. Yet, there was no increase of grooming within the dyad with decreasing rank distance and high ranking individuals were not competed over at the highest rates. The observed correlation between grooming and support received represents an important fit with Seyfarth's prediction, but does not allow for conclusions about underlying causal processes. Other causal explanations, besides the 'groom to receive support' hypothesis, that could explain a similar correlation are discussed.

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Introduction

Social grooming is considered a key feature in primate social organization. Several functions have been suggested for this behavior. Apart from its hygienic function (Hutchins & Barash, 1976), the interaction is stress reducing (Terry, 1970; Boccia, 1987) and is used in reconciliation, two aspects that are generally considered as central features in bonobo groups (de Waal, 1989). Grooming relationships create bonds that directly affect group cohesion (Dunbar, 1996), and grooming bonds determine the degree of familiarity and predictability of each other's behavior (Dunbar, 1988, p. 254), a factor that is known to be important for the efficient use of coalitions (Colvin, 1983). Seyfarth (1977) elaborated on the role of grooming in a functional exchange process of social services and suggested specifically that primates groom in order to receive support.

As in most group living primate species, the distribution of grooming among bonobos is related to several variables, such as kin, sex, age and rank. We present a review of the literature. Data on bonobo grooming come predominantly from studies on free-ranging bonobos. In general, there is relatively more intra-sexual grooming in small parties — particularly among females — and more inter-sexual grooming in larger parties (Kuroda, 1979, 1980; Kano, 1982, 1992; Kitamura, 1983; Kano & Mulavwa, 1984; Furuichi, 1987, 1989; White, 1992; White & Lanjouw, 1992; review Van Elsacker *et al.*, 1995). When the frequency of inter-sexual grooming is high, male intra-sexual grooming tends to decrease (Muroyama & Sugiyama, 1994). Furuichi (1989) found that the high incidence of mixed sex grooming was due to mother-son interactions. With regard to the variables rank and age, Idani (1991) notes that especially old, high ranking adult females are the preferred grooming partners of newly immigrated females.

Captive studies are limited by the fact that bonobos are rare and that only few captive groups mimic a 'natural' group composition, *i.e.* several adult males and females and their dependent offspring. In a small ($N = 4$) captive group at the Yerkes Primate Research Center the high female intra-sexual bonding (Blount, 1990) corresponds to the pattern seen in small parties ($N < 6$) in Lomako, Zaire (White, 1992; White & Lanjouw, 1992).

In the captive groups at the San Diego Zoo, Frankfurt Zoo, and Stuttgart Zoo, containing 5 or less, 5 and 4 adult (and several younger) individuals respectively, Parish (1996) found that females preferentially selected females over adult male group members as groomees. For the groups of the Wild Animal Park Planckendael, Stuttgart Zoo and Wuppertal Zoo, containing 4, 3 or 4, and 4 adult (and several younger) individuals respectively, Franz (1998, 1999) found that high ranking adult females received significantly more grooming and low ranking subadult males and females received least, whereas the latter initiated most grooming sessions. Overall, the literature survey indicates that bonobo grooming distributions are variable and are partially related to variables such as sex, group size and composition, age, kin and rank. There are some indications that females, higher ranking animals and older animals are the preferred grooming partners.

Models that aim to explain grooming relationships that show a rank-related distribution have been formulated by Seyfarth (1977) and by de Waal & Luttrell (1986). Seyfarth (1977) observed that in several primate groups higher ranking animals received more grooming than others, and the majority of grooming occurred between individuals of adjacent rank. To explain these observations Seyfarth (1977, 1980) suggested that individuals compete for grooming access to higher ranking individuals since the latter are the best coalition partners. As a consequence of this, most grooming will go up the hierarchy. As a result of this, competition will arise, leading to a monopolization of high ranking individuals by the individuals ranking just below them, so that most grooming will occur among adjacent ranks in the hierarchy. The principle that social interactions can be interchanged for one another, as elaborated by Seyfarth, was later generalised in Noë & Hammerstein's (1995) 'biological market model'. Market forces were used to predict grooming interactions by Barrett *et al.* (1999) and Henzi & Barrett (1999) who found interchange of grooming with other commodities to occur only in groups with linear hierarchies.

Alternatively, de Waal & Luttrell (1986) suggest that a rank-related grooming distribution can be more parsimoniously explained as being due to the preference of the females to groom individuals with similar characteristics, such as for instance rank, social class, sex, age or kin, which is suggested as an adaptive strategy because such coalitions offer the greatest likelihood of compatibility. This principle could account for grooming between individuals of adjacent ranks, regardless of kin (de Waal & Luttrell, 1986; Parr *et al.*,

1997). Kin selection can be an important explanatory factor for the distribution of grooming bonds in groups where degrees of relatedness are known to differ such as for instance in the study by de Waal & Luttrell (1986) and Seyfarth *et al.* (1978). In our study group where all animals can be considered unrelated (Table 1), kin selection can not be invoked as explanation of the grooming relationships. Seyfarth's model was originally formulated for female intra-sexual grooming bonds in several species of Old World monkeys, some of which are characterized by the presence of only one male (*e.g. Theropithecus gelada*). Bonobo groups usually contain several males and females in a party, among which frequent grooming bonds are maintained (*e.g.* Kano, 1992). To justify the application of Seyfarth's model on a mixed-sex group, the effect of the variable sex upon the distribution of grooming bonds has to be taken into account.

We formulated the following goals for our study: (1) to examine the relative effect of the three variables sex, age and rank on the distribution of bonobo grooming; (2) to examine whether Seyfarth's model or de Waal & Luttrell's similarity principle could best account for the observed distribution of grooming. We tested assumptions and predictions for both models. This analysis was carried out in a study group that mimics the size and composition of natural groups to a certain extent, *i.e.* containing several adult males and females and their dependent offspring. Since all adult animals can be considered unrelated, the effect of the variable kin does not need to be taken into account.

Methods

Study group

The Planckendael group was observed between 10 October 1992 and 16 February 1993 for 16264 minutes. Observations covered most of the active day (*i.e.* from breakfast till the evening meal), which ensured that all grooming bouts and support acts were observed from the onset of activity. All individuals remained within sight throughout the day. Complex interactions were filmed. The composition of the study group is shown in Table 1 (Van Elsacker *et al.*, 1993).

Observational methods and analysis

A. Behavioral sampling

The frequency and duration of grooming bouts was noted for each adult individual ('all occurrences sampling' and 'focal sampling': Altmann, 1974). In a grooming bout the

TABLE 1. *Composition of the study group of bonobos in the Wild Animal Park Planckendael, Belgium*

Name	Sex	Birth	Age (in 1993[1])	Origin	Rank[2]
Dzeeta	Female	1971[3]	Approx. 22	Wild	6
Hermien	Female	1978[3]	Approx. 15	Wild	5
Desmond	Male	1971[3]	Approx. 22	Wild	4
Hortense	Female	1978[3]	Approx. 15	Wild	3
Ludwig	Male	26-08-1984	9	Desmond-Dzeeta[4]	2
Kidogo	Male	28-02-1983	10	Masikini-Catherine	1
Redy	Male	24-11-1990	3	Desmond-Hortense	–
Unga	Female	02-02-1993	< 1	Desmond-Hermien	–

The six adult individuals (from Dzeeta up to Kidogo) were the focus of this study.
[1] Leus & Van Puijenbroeck, 1997.
[2] Dominance rank from high (6) to low (1) (Vervaecke *et al.*, 1999, 2000a).
[3] Exact month or day of birth not known.
[4] Ludwig was hand-reared. The biological relatedness between Ludwig and Dzeeta seems not to be recognized by either of the two individuals. There is no expression of a particularly strong affiliation, nor is mating inhibited in this combination as seen in a natural mother-son bond.
– Redy and Unga were still dependent infants and not included in this study. Their rank was not determined.

participation of each active partner was scored once. Subsequent switches between the active and passive role were not counted as new bouts. For instance, in a grooming bout in which Dzeeta first groomed Desmond, who then reciprocated the grooming, it was once scored that Dzeeta was the actor and Desmond the receiver; once that Desmond was the actor and Dzeeta the receiver. Subsequent switches in the same grooming bout are not counted. A grooming bout was finished when no grooming occurred for 30 s since a longer interval tended to be accompanied by other activities. To calculate grooming rates per hour, divide the total grooming frequencies by the observation period: 16264 minutes (271 hrs).

To quantify proximity we conducted 78 scans randomly distributed throughout the day and with at least a 30 minute interval between scans. In each scan, we noted which individuals were within three meters of each other (see Table 3: lower triangular half).

Interventions towards a grooming dyad are defined as: pestering and aggressions towards a grooming dyad irrespective of the result, as well as interactions where two individuals were grooming, a third animal approached and supplanted one of the groomers, and the remaining two then started grooming (analogous to Seyfarth, 1980, p. 803).

Approaches leading to grooming were scored if no interactions of a different kind intervened in the period between the approach and the onset of grooming.

Support is defined as all the instances where an individual intervenes with an aggression (excluding pestering but including directed vocalizations) within 30 s upon an agonistic interaction (including pestering) between at least two other individuals to aid in attack and/or in defense. In case this behavior was repeated within 30 s it was scored only once. (A directed vocalization was only scored in instances where the individual was visually monitoring

TABLE 2. *Matrix of aggressions or opportunities to support**

	Receiver						
	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Actor:							
Dzeeta	–	4	6	7	16	53	86
Hermien	4	–	9	3	9	26	51
Desmond	7	28	–	3	1	33	72
Hortense	0	2	0	–	228	11	241
Ludwig	0	0	0	85	–	6	91
Kidogo	31	27	67	2	13	–	140
Total	42	61	82	100	267	129	

* Including aggressions used to determine rank, and including pestering.

the recipient in a prolonged and obvious manner, while vocalizing aggressively, loudly and intensely, during agonism with coalitionary support.)

In instances where aid in attack is given in an interaction with several aggressors, the aid is directed to the individual or the individuals that aggressed the same victim prior to the act of support (also called 'pro-intervention': de Waal & Luttrell, 1986). During aid in defense, the aggression towards an initial attacker, is seen as a support for the individual that has been aggressed in the initial interaction (also called 'contra-intervention': de Waal & Luttrell, 1986). In cases where several individuals have aggressed simultaneously prior to the act of support, the aid is directed to each of the individuals that were aggressing. When supporters join in a fight after more than one individual was involved in the supporting action, we defined that they support the individual that had started to support just prior to them. The individual that receives the agonism from the actor of support is the receiver of contra-support.

In this study, we included co-operative redirections (two animals that were involved in an initial conflict with each other aggress the same individual simultaneously or in sequence) as support. For the analyses support was not spliced in aid in defense and attack (pro and contra interventions) since there occurred relatively little aid in defense so that many entrees remained blank in the matrix.

Frequencies of support were divided by the number of opportunities an individual had to give support and multiplied by 100. Individual A's opportunity to support individual B by intervention in a conflict with B is defined as the number of conflicts that B had with individuals other than A, as in Hemelrijk & Ek (1991).

In the matrix of opportunities to support (see Table 2) we included all the aggressions (*i.e.* short and long charges, intention movements, directed displays, pestering aggression) and pestering, all with or without contact, regardless of the reaction of the opponent. Pestering was defined as an opportunity to offer support, due to its harassing nature, yet it was not considered an act of support, given its undecisive nature.

B. Dominance hierarchy

Dominance relationships were determined by using directions of submissive behavior (*i.e.* fleeing upon aggression and peering) performed during the same period of observation when

the animals were not part of an act of agonistic support (Vervaecke *et al.*, 2000a). Since the linearity in the set of dominance relationships is complete and significant in the Planckendael group (Landau's $h = 1$, $p = 0.022$; Appleby, 1983), the individuals could be ordered into a linear hierarchy and each individual unambiguously assigned a rank. The ranks are shown in Table 1. Ranks are presented from 6 (highest ranking animal) to 1 (lowest ranking animal) to facilitate the presentation of correlations with the variable rank.

C. Statistical procedures

The proportions of grooming frequencies and duration were similar ($\tau_{rw} = 0.876$, $p = 0.003$, rowwise correlation of number of observed grooming events over the study period with duration of observed grooming events over the study period) and therefore only the frequencies are used for further statistical analysis. A comprehensive analysis with the dyad as the statistical (observational) unit of analysis was performed using the rowwise matrix correlation method — developed by Hemelrijk (1990a, b) and by de Vries (1993) — in order to determine the relative effect of the variables sex, rank, age and proximity on grooming and being groomed. A definite advantage of matrix correlation methods as compared with statistical methods that take the individual as the observational unit of analysis, is that dyadic variation is taken into account. Moreover, rowwise matrix correlation methods control for differences in the row totals. For instance, if the row individuals are the groomers then the differences among the individuals in their tendencies to groom is controlled for. Kendall's form of rowwise matrix correlations (τ_{rw}) and exact right-tailed probability values (p_r) or in case of negative correlations, left-tailed probability values (p_1) were calculated with MatMan, a program for the analysis of sociometric matrices (de Vries *et al.*, 1993). To determine the relative importance of each factor on the grooming behavior, a partial correlation analysis was performed in order to keep the effect of a specific factor (*e.g.* sex) constant (which is thus 'partialled out' or 'controlled for') while calculating the correlation between two other factors (*e.g.* grooming and rank). Using the MatMan program, Kendall's form of partial rowwise matrix correlation ($\tau_{rw;XY.Z}$) was calculated. A limitation is that one cannot partial out multiple factors. Twenty thousand random permutations were carried out to obtain accurate estimates of the p-values (following the advice of Jackson & Somers, 1989) of the partial rowwise correlations. A two-tailed p-value smaller than 0.05 was considered statistically significant. In case of significance, the row correlations were checked per individual to assure that the result was not due to the scores of a few individuals only.

A dyadwise matrix correlation test based on Kendall's τ_a-correlation was used to determine whether there is more grooming up the hierarchy than down the hierarchy. Whereas a rowwise matrix correlation is based on all those pairs of cells that have a row individual in common, a dyadwise correlation coefficient is based on those pairs of cells that have a row individual *and* a column individual in common (de Vries, 1998).

To find out whether the total number of grooming acts among pairs of animals is greater when they are closer in rank to each other, the agreement between the rank distance matrix and the dually normalized symmetric grooming matrix was assessed by means of the rowwise K_r test. In order to take individual differences in the tendency to be involved in grooming (as groomer or as groomee) into account, the symmetric grooming matrix, which contains for each dyad the sum of the grooming interactions in both directions, has been dually normalized by means of fitting homogeneous margins (Freeman *et al.*, 1992). By means of an iterative proportional fitting method the counts in the matrix are scaled to fit equal margins (as an example we show in the upper triangular half of Table 3 the dually normalized values of the

TABLE 3. *Proximity matrix/dually normalized values of proximity*

	Dzeeta	Hermien	Desmond	Hortense	Ludwig	Kidogo	Total
Dzeeta	–	34.4	12.9	16.6	13.6	22.6	100
Hermien	10	–	15.9	22.4	24.4	2.8	100
Desmond	8	2	–	14.0	25.8	31.5	100
Hortense	22	6	8	–	20.1	27.0	100
Ludwig	11	4	9	15	–	16.1	100
Kidogo	10	0	6	11	4	–	100
Total	61	22	33	62	43	31	

This table contains two triangular halfs of two symmetric matrices. Below the diagonal: matrix of proximity counts. Above the diagonal: the dually normalized values of these proximities. The column totals give the marginal totals of the full matrix of proximity counts. The row totals give the marginal totals of the full matrix of the dually normalized values.

proximity counts scaled to fit margins of 100). For the purpose of testing de Waal & Luttrell's similarity principle, the symmetrized grooming matrix and the proximity matrix have been dually normalized in the same way. Subsequently, correlations between these and three other symmetric matrices (*viz.* the age difference, rank distance and sameness of sex matrices) were assessed by means of rowwise K_r tests.

To find out whether pairs of animals groom each other more reciprocally when they are closer in rank to each other, we first calculated for each dyad the degree of reciprocal grooming according to the following formula:

$$R_{ij} = 2 * \mathrm{Min}(X_{ij}, X_{ji})/(X_{ij} + X_{ji}),$$

where X_{ij} is the number of grooming acts from individual i to individual j (Seyfarth, 1980, p. 808). Subsequently, the agreement between the rank distance matrix and the symmetric matrix containing the dyadic grooming reciprocities was assessed by means of the rowwise K_r test.

All matrix correlation tests in this paper are based on Kendall's type of correlation coefficient rather than on a Pearson correlation, because the grooming distribution is relatively skew and contains some rather extreme values. As has been noted in de Vries *et al.* (1993, Appendix B), extreme or outlying values can strongly influence the outcome of a matrix correlation test that is based on the Pearson correlation coefficient. All *p*-values presented in this paper are two-tailed.

Results

A. Testing Seyfarth's model

1) Grooming and rank

Table 4 presents the dyadic grooming data (4a: grooming given; 4b: transposed matrix, grooming received). Table 4 also presents the results of the

TABLE 4A. *Frequency of grooming*

	Receiver						Rank	Age	Sex
	Dz	He	Des	Ho	Lu	Ki			
Actor:									
Dzeeta	–	24	41	11	1	0	0.80	0.74	0.26
Hermien	22	–	1	19	0	0	0.74	0.67	0.82
Desmond	48	8	–	40	2	0	0.80	0.74	0.77
Hortense	83	63	40	–	9	1	1.00	0.53	0.77
Ludwig	23	6	15	55	–	6	0.11	0.35	0.41
Kidogo	89	19	8	9	6	–	0.80	0.45	0.77
						τ_{rw}	0.71	0.58	0.64
						p	0.022	0.088	0.10

The correlations per individual with the variables rank, age and sex are shown in the three last columns.
τ_{rw}: Kendall's rowwise matrix correlation. p: two-tailed probability of τ_{rw}.

TABLE 4B. *Transposed grooming matrix*

	Actor						Rank	Age	Sex
	Dz	He	Des	Ho	Lu	Ki			
Receiver:									
Dzeeta	–	22	48	83	23	89	– 0.60	– 0.11	– 0.26
Hermien	24	–	8	63	6	19	0.20	0.32	0.77
Desmond	41	1	–	40	15	8	0.40	0.32	0.26
Hortense	11	19	40	–	55	9	– 0.20	– 0.11	– 0.26
Ludwig	1	0	2	9	–	6	– 0.60	– 0.22	– 0.26
Kidogo	0	0	0	1	6	–	– 0.84	– 0.80	– 0.31
						τ_{rw}	– 0.26	– 0.07	0.00
						p	0.30	0.84	1.0

The correlations per individual with the variables rank, age and sex are shown in the three last columns.
τ_{rw}: Kendall's rowwise matrix correlation. p: two-tailed probability of τ_{rw}.

rowwise matrix correlation analyses to test for the effects of rank, age and sex on grooming and being groomed. These correlation analyses are shown in the three last columns of Tables 4a (grooming given) and 4b (grooming received).

Only between rank and grooming a high and significant correlation is found ($\tau_{rw} = 0.71$; $p = 0.022$): individuals groom high ranking individuals

TABLE 5. *Partial rowwise matrix correlations*

Matrix X	Matrix Y	Matrix Z	$\tau_{rw;XY}$	$\tau_{rw;XZ}$	$\tau_{rw;YZ}$	$\tau_{rw;XY.Z}$	p
Grooming	age of groomee	rank	0.58	0.71	0.65	0.23	0.532
Grooming	age of groomee	sex	0.58	0.64	0.37	0.49	0.156
Grooming	sex of groomee	rank	0.64	0.71	0.60	0.37	0.340
Grooming	sex of groomee	age	0.64	0.58	0.37	0.55	0.174
Grooming	rank of groomee	age	0.71	0.58	0.65	0.54	0.090
Grooming	rank of groomee	sex	0.71	0.64	0.60	0.53	0.098

$\tau_{rw;XY.Z}$: partial Kendall rowwise correlation between matrices X and Y controlled for Z.
p: probability.

more frequently than low ranking ones. Moderate but non-significant correlations are found for age and grooming ($\tau_{rw} = 0.58$) and sex and grooming ($\tau_{rw} = 0.64$). Rowwise correlations between grooming received and rank, age and sex (Table 4b) are all low and non-significant.

Correlations among the three individual variables rank, age and sex are, although non-significant, not negligable: between age and rank: $\tau = 0.65$ ($p = 0.12$); between sex and rank: $\tau = 0.60$; ($p = 0.2$); between age and sex: $\tau = 0.37$ ($p = 0.5$). Therefore, since the individual variables rank, age and sex are not completely independent from each other in our study group, it is necessary to examine in how far each of the three correlations of rank, age and sex with grooming might be due to one of the other variables. To this end we calculated partial rowwise correlations, which are presented in Table 5 (see also Fig. 1).

When the effect of rank is partialled out, the partial correlation between age and grooming drops from 0.58 to 0.23, indicating that the correlation between grooming and age is mainly due to the correlations of rank with both age and grooming. When, on the other hand, the correlation between grooming and rank is controlled for age, the correlation drops also (from 0.71 to 0.54), but not as much as the other way around, indicating that the correlation between rank and grooming is somewhat, but not very much due to the factor age.

Similar conclusions can be drawn with respect to the factor sex. When the effect of rank is partialled out, the partial correlation between grooming and sex drops from 0.64 to 0.37, indicating that the correlation between grooming and sex is mainly due to rank. When, on the other hand, the correlation between grooming and rank is controlled for sex, the correlation drops also

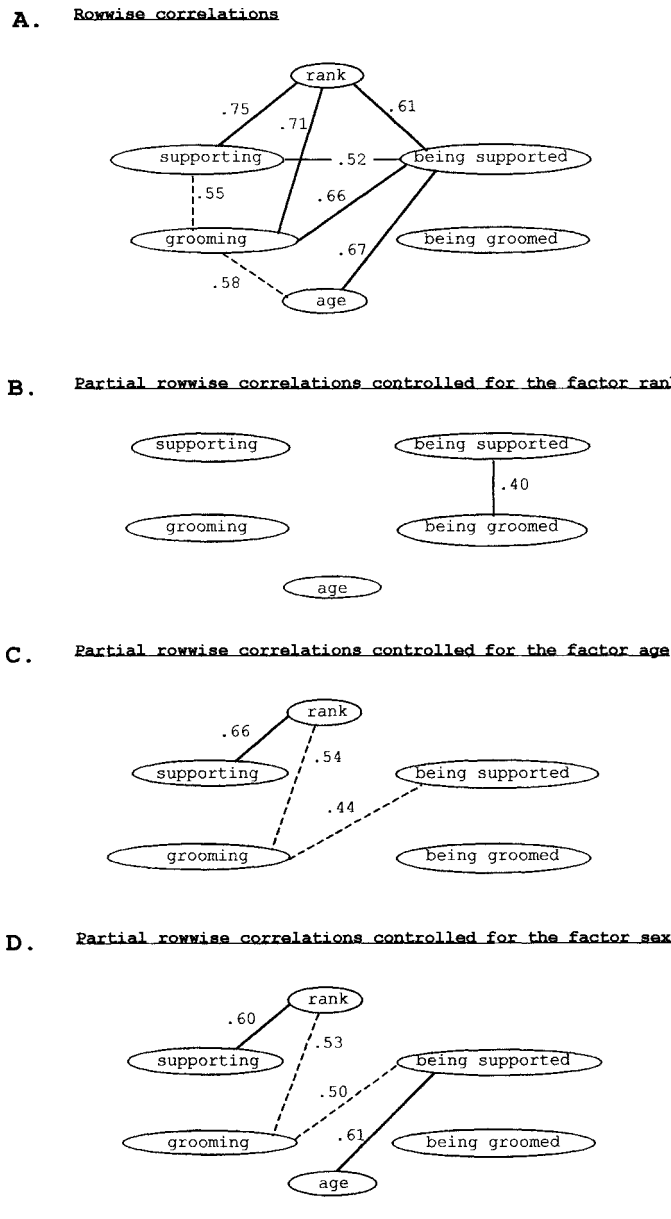

Fig. 1. A: Rowwise matrix correlations between supporting and grooming and the rank and age of the receiver, as well as between being supported and being groomed and the rank and age of the actor. B, C, D: Partial rowwise matrix correlations. Full lines indicate significant correlations ($p < 0.05$); dotted lines $0.05 \leq p < 0.1$.

TABLE 6A. *Matrix of support (as % of opportunities to give support)*

	Receiver						Rank	Age	Sex
	Dz	He	Des	Ho	Lu	Ki			
Actor:									
Dzeeta	–	28.9	6.4	1.2	0.9	2.2	0.60	0.53	0.26
Hermien	16.7	–	1.7	1.8	0.3	0	0.80	0.53	0.77
Desmond	19.1	20.0	–	2.1	0	0	0.74	0.67	0.82
Hortense	5.8	7.5	1.3	–	2.2	0	0.60	0.11	0.77
Ludwig	1.8	1.0	0.7	0	–	0	0.95	0.59	0.41
Kidogo	4.5	1.7	0	0	0	–	0.84	0.40	0.62
						τ_{rw}	0.75	0.47	0.61
						p	0.006	0.176	0.200

The correlations per individual with the variables rank, age and sex are shown in the three last columns.
τ_{rw}: Kendall's rowwise matrix correlation. p: two-tailed probability of τ_{rw}.

(from 0.71 to 0.53), but not as much as the other way around, indicating that the correlation between rank and grooming is somewhat, but not very much due to the factor sex.

Overall, these correlations show that rank had the greatest impact on grooming in our study group: individuals preferentially groom higher ranking group members. Only the male Ludwig distributes its grooming not according to the rank of the groomee.

2) Exchange of grooming for support

The main assumption of Seyfarth's model is that animals that groom others will receive support in return. This assumption is clearly confirmed in our bonobo group: the rowwise correlation between the grooming matrix (Table 4a) and the receipt of support matrix (Table 6b) is highly significant ($\tau_{rw} = 0.66$; $p = 0.008$).

As can be seen from Table 7, which presents the Kendall τ values for each individual, each bonobo (with the possible exception of Desmond) clearly distributes its grooming in relation to the amount of support received. Since this exchange relation between grooming and receipt for support might be due to correlations of these behaviors with other variables (rank, age, sex) we also computed partial correlations. To this end we first calculated the rowwise correlations between support given and the rank, age and sex of the receiver of the support (Table 6a), as well as between support received and

TABLE 6B. *Transposed matrix of support*

	Actor						Rank	Age	Sex
	Dz	He	Des	Ho	Lu	Ki			
Receiver:									
Dzeeta	–	16.7	19.1	5.8	1.8	4.5	0.60	0.95	0.26
Hermien	28.9	–	20.0	7.5	1.0	1.7	0.80	0.95	0.52
Desmond	6.4	1.7	–	1.3	0.7	0	1	0.74	0.77
Hortense	1.2	1.8	2.1	–	0	0	0.32	0.67	0.27
Ludwig	0.9	0.3	0	2.2	–	0	0.32	0.12	0.82
Kidogo	2.2	0	0	0	0	–	0.63	0.53	0.41
						τ_{rw}	0.61	0.67	0.51
						p	0.026	0.011	0.300

The correlations per individual with the variables rank, age and sex are shown in the three last columns.
τ_{rw}: Kendall's rowwise matrix correlation. p: two-tailed probability of τ_{rw}.

TABLE 7. *Kendall correlation between grooming given and support received for each individual*

	Kendall τ between grooming and being supported
Dzeeta	0.80
Hermien	0.74
Desmond	0.32
Hortense	0.80
Ludwig	0.63
Kidogo	0.67
τ_{rw}	0.66
p	0.008

the rank, age and sex of the supporter (Table 6b). In Fig. 1A we present a diagram with all significant correlations ($p < 0.05$) and those which come close to significance ($0.05 \leqslant p < 0.10$). We will first discuss these correlations and then consider whether the correlations between grooming and support (given or received) might be due to correlations with the individual variables rank, age and sex.

The rank of the supported individual is highly and significantly correlated with the amount of support given (expressed as the % of opportunities to give support): each bonobo gives more support to high ranking others ($\tau_{rw} = 0.75$, $p = 0.006$; Table 6a). Also the rank of the supporter is correlated with the

support received: each bonobo is more supported by high ranking others (τ_{rw} = 0.61, p = 0.026; Table 6b). The age of the supporter is also significantly correlated with receipt of support: individuals receive more support from older supporters (τ_{rw} = 0.67, p = 0.011; Table 6b). Sex was not significantly correlated with either giving or receipt of support.

Since, moreover, the existence of a grooming for support relation could also be due to reciprocity in grooming and/or reciprocity in support among the animals, we calculated the rowwise correlations between grooming and being groomed (τ_{rw} = 0.05; p = 0.86) and between support and being supported (τ_{rw} = 0.52; p = 0.038).

The next step is to compute partial rowwise correlations. Diagrams B, C and D in Fig. 1 show the partial rowwise matrix correlations controlled for the variables rank, age and sex, respectively. The first thing to note when these partial correlations are compared with the correlation values in Fig. 1A, is that the correlation between grooming and received support decreases from a significant value of 0.66 (p = 0.008) to non-significant values of 0.40 (p = 0.136), 0.44 (p = 0.098) and 0.50 (p = 0.060) when rank, age or sex is partialled out, respectively. So, part of the correlation between grooming and received support is due to rank, age, or sex, but clearly this correlation is not completely spurious. The other two behavior correlations in Fig. 1A, between supporting and being supported (τ_{rw} = 0.52; p = 0.038) and between supporting and grooming (τ_{rw} = 0.55, p = 0.05), disappear almost fully when controlled for each of the variables rank, age, or sex. The first one, the reciprocity in support, drops to non-significant values of 0.13, 0.27, 0.31, when controlled for rank, age or sex, respectively. The low correlation of 0.13 when rank is partialled out indicates that the reciprocity in support is due to correlations of support given and support received with rank. The other correlation, between supporting and grooming, drops to non-significant values of 0.03, 0.33, 0.27, when controlled for rank, age or sex. Here also we see that it is mainly rank that is responsible for the high correlation between supporting and grooming.

The next thing to note is that when rank is controlled for (Fig. 1B), the correlation between age and being supported (τ_{rw} = 0.67, p = 0.011) drops to a non-significant value of 0.46 (p = 0.12). When, on the other hand, sex is controlled for (Fig. 1D), this correlation decreases only slightly to a value of 0.61 which is still significant (p = 0.036). So, here also rank is the more important factor. As a final indication of the pivotal role of

rank in grooming and support behavior, we found that controlling for rank revealed the existence of a previously masked correlation between being supported and being groomed ($\tau_{rw;XY.Z} = 0.40$, $p = 0.036$) (see Fig. 1B). So, individuals that receive more support from others are also more groomed by these others, independent of the rank of these others. This result could imply the existence of a for as yet unknown service that might be returned by the receivers of grooming and support.

3) Up-hierarchy grooming

Not only did every individual (except Ludwig) distribute its grooming according to the rank of the groomee, but also within each dyad grooming was rank-related. In line with Seyfarth's prediction, up-hierarchy grooming occurred significantly more often than down-hierarchy grooming (dyadwise matrix correlation test: $\tau_{a;dw} = 0.73$, $p = 0.04$).

4) Competition over grooming

Most of the observed interventions towards grooming dyads (67%, 58 out of 86) occurred in dyads of a subordinate grooming a dominant individual. In the same line, 92% (267 out of 289) of the approaches leading to grooming were made by the lower ranking of the resulting dyad, in accordance with Seyfarth's model. When the number of interventions towards a groomed individual were corrected for the frequencies of received grooming, there was no significant positive correlation between the rank of the individual and the rate at which it was competed over ($r_s = 0.43$, $N = 6$, NS). According to Seyfarth's model (Seyfarth, 1980), the highest ranking individuals should be able to distribute grooming in direct relation to the rank of the others, whereas the mid and lower ranking individuals will be more constrained by competition resulting in a lower correlation between grooming and the rank of others. This was not so in the study group (see Table 4b).

5) Grooming among adjacent ranks

There was no significant correlation between the rank distance and the total number of grooming interactions within a dyad: the rowwise matrix correlation between the dually normalized grooming matrix and the rank distance matrix was very low and non-significant ($\tau_{rw} = 0.04$; $p = 0.95$). The 17 cases of competition over grooming which resulted in a new grooming dyad, did not systematically lead to an increase in grooming

among individuals of close rank, contrary to Seyfarth's prediction. However, another prediction of Seyfarth's model (1980, p. 808) was fulfilled. A strong and significant correlation was found between the degree of reciprocal grooming within a dyad and the rank distance between the members of this dyad ($\tau_{rw} = -0.69$, $p = 0.012$). Individuals close in rank to each other groom each other more reciprocally.

6) Groom-contra-support

When examining Seyfarth's model, de Waal & Luttrell (1986) suggested to examine contra-support also: if grooming would correlate with support received and also with contra-support received, there would be no net benefit, weakening Seyfarth's model. In our study group grooming does not decrease the receipt of contra-support ($\tau_{rw} = -0.04$; $p = 0.92$). Neither is the amount of grooming received by a bonobo correlated with the amount of contra-support directed against this groomer ($\tau_{rw} = 0.28$, $p = 0.18$). Choosing someone as a victim of contra-support more often does not decrease the tendency to groom that individual ($\tau_{rw} = -0.051$; $p = 0.84$). Individuals being chosen as a victim by someone more often, tend somewhat to get less grooming of that individual ($\tau_{rw} = -0.53$; $p = 0.11$). Since grooming did not correlate significantly with contra-support received, the argument that could weaken Seyfarth's model is not supported.

B. Testing the similarity hypothesis

The similarity hypothesis predicts that animals prefer to establish bonds with individuals of like traits. Therefore a negative correlation is expected between proximity and relative age difference, between proximity and rank distance, and between proximity and sameness of sex within a dyad. However, none of these correlations were significant (Table 8, proximity-age difference: $\tau_{rw} = 0.26$, $p = 0.27$; proximity-rank distance: $\tau_{rw} = 0.04$, $p = 0.88$; proximity-sameness of sex $\tau_{rw} = 0.39$, $p = 0.20$). Note that before calculating these correlations the proximity matrix has been dually normalized (see Methods and Table 3). The similarity hypothesis also predicts more grooming between individuals of like age, sex or rank. Here also, none of the correlations were significant (Table 8: grooming-age difference: $\tau_{rw} = -0.18$, $p = 0.51$; grooming-rank distance: $\tau_{rw} = 0.04$, $p = 0.94$; grooming-sameness of sex $\tau_{rw} = 0.00$, $p = 1.0$). Finally,

TABLE 8. *Rowwise matrix correlations between symmetric matrices*

Matrix X	Matrix Y	$\tau_{rw;XY}$	p
Proximity	age difference	0.26	0.27
Proximity	rank distance	0.04	0.88
Proximity	sameness of sex	0.39	0.20
Grooming	age difference	– 0.18	0.51
Grooming	rank distance	0.04	0.94
Grooming	sameness of sex	0.00	1
Proximity	grooming	– 0.17	0.58

$\tau_{rw;XY}$: Kendall rowwise matrix correlation. p: probability.
Proximity matrix is dually normalized.
Age difference: relative age difference.
Grooming: amount of grooming summed within a dyad and then dually normalized.
Sameness of sex: same-sex dyad: 1; mixed-sex dyad: 0.

according to the similarity hypothesis, proximity should correlate positively with the amount of grooming within a dyad, which is however not the case ($\tau_{rw} = -0.17$, $p = 0.58$). Note that before calculating these correlations the grooming matrix has been dually normalized.

Discussion

The aim was to examine to which theoretical model the observed grooming distribution best corresponds. With regard to the relative effect of rank, age and sex on grooming we suggest that sex and age are mainly indirectly related to grooming, namely via their effect on rank. From the partial correlations found (Figs. 1B, C, D) one can infer the following most likely causal pathways with respect to grooming: sex and age influence rank and rank influences grooming. Several predictions of Seyfarth's 'grooming for support' model were confirmed: the individuals preferred to groom higher ranking individuals, overall most grooming went up the hierarchy, and there was a significant correlation between grooming given to a groomee and support received from the latter. This confirms the findings of Barrett *et al.* (1999) that grooming was interchanged for access to rank related commodities such as support, in groups in which dominance relations are strongly expressed. In the same line of reasoning Henzi & Barrett (1999) predict grooming between individuals with a low power differential to be more reciprocal, a pattern also observed in our study: grooming reciprocity within a dyad was

stronger according to the rank distance being smaller. Increased total grooming among adjacent ranks, however was not confirmed. Seyfarth's model also holds that the competition over grooming partners can be so fierce that subordinates have to content with lower ranking groomees, resulting in more frequent grooming among adjacent ranks. There was overall no convincing evidence that high ranking individuals were most competed over. Possibly the competition which we observed had only a limited effect on the grooming availability of the higher ranking individuals due to the small group size with consequential limited possibility to monopolize individuals throughout the entire day, as suggested by Sambrook *et al.* (1995). Franz (1999) similarly found in four captive bonobo groups no evidence for competition over grooming access to high ranking individuals, but as predicted by the model, high-ranking females received most allogrooming.

The similarity hypothesis predicts that individuals establish bonds with individuals to whom they most resemble. Since the animals did not prefer the company of individuals of like rank or age, and since they neither preferred to groom individuals of like rank or age, the similarity hypothesis could not be confirmed. Further, being in close proximity of another individual did not increase the probability of getting involved in grooming interactions with this individual. In addition, the similarity model does not invoke an exchange of services, as observed in the study group.

De Waal & Luttrell (1986) suggested that there would be no net benefit in the exchange of the grooming for support in case grooming would also correlate with contra-support received. This was however not the case in this study. On the other hand, grooming did also not prevent the receipt of contra-support.

When rank was controlled for, a correlation was detected which had been masked by the effect of rank. We found that if the animals tended to be supported more by an individual they also tended to be groomed more by the latter. Possibly, this uni-directional favoring of certain individuals, independent of their ranks, indicates that these individuals can provide some other for as yet unknown service in return.

The observed correlation between grooming given and support received represents a crucial fit with Seyfarth's model. However, as is well known, one has to be cautious in interpreting the results of correlational analyses. From a given correlation, one can not draw any conclusion about the underlying causal processes. We can not conclude that proof is given for the fact that the

animals do X *in order to* receive Y. There can be many different causal chains between grooming given, grooming received, support given and support received and these may not always be revealed by correlations (Seyfarth, 1991). Moreover, the analysis is restricted to a limited number of behaviors and it is likely that primates take multiple other interactions into account when making their social exchange balance. When discussing the results of our study, we have to take into consideration that besides the 'groom to receive support'-hypothesis, several causal processes would predict a similar correlation. First, the individuals may directly tune the support which they give to a certain individual to the grooming the latter just gave to them. Second, the exchange may be the effect of a number of other processes. Hemelrijk (1990) argues that a similar correlation between grooming and receipt of support — which she found in common chimpanzees (Hemelrijk & Ek, 1991) — would be expected in case individuals groom higher ranking individuals more often, to protect themselves from their aggression (as suggested by Silk, 1982 and by Henzi & Barrett, 1999) and when higher ranking individuals are more inclined to support whomsoever to maintain their dominance rank. In order to test the strength of Hemelrijk's hypothesis of 'groom to avoid aggression' and 'support to maintain rank', a specific prediction was tested in our study group. In line of her reasoning there should be a negative correlation between grooming given and aggression received, at least if the animals were successful at this strategy. This was however not the case in our study group (Kendall rowwise correlation between grooming given and aggression received: $\tau_{rw} = 0.23$; $p = 0.24$). The observations on the study group did fit the latter part of the hypothesis (support to maintain rank) (Vervaecke *et al.*, 2000b).

Hemelrijk (1991) suggested that when other processes result in a similar correlation, they should be preferred as more parsimonious explanations to the hypothesis of an exchange of social services which would require complex cognitive capacities. In reply to Hemelrijk, Seyfarth (1991) argues that one does not necessarily need to explain the interchange relationship as a spurious by-product due to two other unrelated processes. Even if a correlation does not appear 'genuine' due to its correlation with other factors, there could be a valid exchange relationship. For instance, an individual who is deciding to groom an animal may pick out an individual who is likely to be a good coalition partner. Here rank is a good criterion of choice that allows to

predict who is likely to be a good coalition partner. In our study the correlation between grooming given and support received could be due to the almost significant correlation between grooming given and support given (τ_{rw} = 0.55, p = 0.05) and the reciprocity in support (τ_{rw} = 0.52) (see Fig. 1A). In such a case, Seyfarth (1991) argues that receivers of grooming use this behavior (grooming given) as a criterion for deciding whom to support.

In conclusion, our data support Seyfarth's hypothesis: the bonobos in our study group appear to groom each other to receive support. Possibly, animals may groom higher ranking partners partly to reduce tension as an immediate benefit (Terry, 1970; Boccia, 1987) and get the additional benefits of increased support from the best coalition partners. The data do not fit the more parsimonious similarity principle as formulated by de Waal & Luttrell (1986). Considering the limits at correlational methods, more solid proof of the existence of exchange relationships (reciprocity or interchange) would consist of a temporal sequential link between the behaviours. However, since we do not know the time-scale which the animals use in their social exchanges (Hemelrijk, 1991), it is difficult to determine what time blocks need to be analyzed. Further, it is difficult to determine whether and how other behaviors upset the exchange balance (Seyfarth & Cheney, 1988). An experimental search for a temporal link between grooming and support was undertaken by Seyfarth & Cheney (1984) who found that unrelated animals looked up sooner upon distress-calls of individuals if they had previously been groomed by the individual that needed support. Hemelrijk (1994) found that females supported others significantly more often after being groomed by them in the recent past than in the cases without prior grooming. Chapais *et al.* (1995) found experimental proof for the affiliation for support hypothesis in the temporal sequence of behaviors performed in newly formed subgroups, suggesting that animals compete for affiliation with dominants to obtain their support not just against anyone but specifically against lower-ranking individuals in order to maintain their rank. Support for the latter version of Seyfarth's hypothesis also comes from our study on the distribution of the coalitions, which suggests that coalitions are used for rank maintenance in the study group (Vervaecke *et al.*, 2000b). Solid experimental evidence of sequences of partner-specific service exchange in nonhuman primates was presented by de Waal (1997) who found that chimpanzees (*Pan troglodytes*) that have previously groomed each other indeed preferentially share provisioned food in the direction opposite of the grooming (*i.e.* after

A groomed B, B shared more with A). So far, we can add the bonobo as a candidate to the list of primates in which some form of exchange relationship was documented and for which further experimental investigation is required to determine the exact nature of this relationship.

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